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THE DEVELOPMENT AND ANATOMY OF SARRACENIA PURPUREA

CONTRIBUTIONS FROM THE BOTANICAL LABORATORY OF THE
JOHNS HOPKINS UNIVERSITY, NO. 5

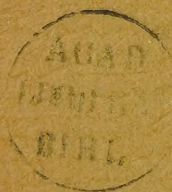
(WITH PLATES III-V)

DISSERTATION

SUBMITTED TO THE BOARD OF UNIVERSITY STUDIES OF THE JOHNS HOPKINS
UNIVERSITY FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

BY
FORREST SHREVE

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PURPUREA.¹

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(WITH PLATES III-V)

THE work of which the results are here given was undertaken at the suggestion of Dr. D. S. JOHNSON, and has been carried out at the Biological Laboratory of the Johns Hopkins University.¹ I wish here to express my thanks to Dr. JOHNSON for much advice and helpful criticism in connection with this work, and to express to Professor WILLIAM K. BROOKS my appreciation of his interest and encouragement. I also wish to thank my fellow-student Mr. SAMUEL RITTENHOUSE for his kindness in gathering material for me during my absence from Baltimore.

The material worked upon was obtained mainly at Glenburnie, Maryland, near Baltimore. Most of it was fixed in the field; and of several killing reagents tried 1 per cent. chrom-acetic and Carnoy's mixture were the most satisfactory. Preparations were made by ordinary paraffin method and stained with the Flemming triple stain or with cyanin and erythrosin.

DEVELOPMENT OF THE FLOWER.

The earliest stage observed in the development of the flower was in material gathered August 30. There are then to be seen the primordia of the three bracts, the five sepals, and the five petals, which have apparently arisen in the order named. Lying just within the edges of the petals are the staminal primordia, as yet mere papillae, and within them is a flat surface with slight elevation at the center. A somewhat later stage than the last shows progress in the development of the stamens, which now appear as ten groups of protuberances lying in the position before noted (*fig. 2*). Each

¹ Dissertation submitted to the Board of University Studies of the Johns Hopkins University for the degree of Doctor of Philosophy.

group arises from a base which is distinct from the bases of the adjoining groups, and is made up of the primordia of five to eight stamens. There is no suggestion of a pairing of the groups nor of their falling in two whorls. Upon the central flat surface has arisen the ovary, which at its base is pentagonal in outline, and at its apex is surmounted at the angles of the pentagon by the tips of the carpellary leaves. The outgrowths of the wall of the ovary which are destined to give rise to the placentae are upon the sides of the pentagon, which shows each placenta to be made up of the edges of two carpellary leaves (*figs. 2, 14*).

MICROSPORANGIUM AND MICROSPORE.

The staminal primordia early show differentiation into parts destined to give rise to filament and anther. The latter portion bears approximately the same outline in cross section as do the mature anthers. The location of the archesporium is indicated at first only by the slightly greater size of the nuclei in the region of the four microsporangia (*fig. 4*), but soon comes to be more sharply defined by the concentric arrangement of cells in the region of the future parietal cells. The archesporium is at this earliest recognizable stage about six cells in cross section, but grows rapidly to about twelve cells in diameter (*fig. 5*). Development proceeds in the autumn to the differentiation of the endothecium, the two or three parietal layers, and the pollen mother cells. There is yet no distinction of definitive sporogenous cells and tapetum. In this condition the stamens pass the winter.

The elongated parietal cells do not contribute to the tapetum, but it is made up entirely from the isodiametric cells of the archesporium. The outer outline of the tapetal layer is continuous, and the inner is irregular only to an extent which makes it in some places two cells in thickness and in other places three. The cells of the tapetum do not wander among the definitive sporogenous cells. Shortly after the differentiation of the tapetum, and before the pollen mother cells are in the synapsis stage, the tapetal nuclei divide once by mitosis, and so far as observed once only. At the time of tetrad division the tapetal nuclei are enlarged, the chromatin is granular and scattered, and the nucleoli are large. At the time of the forma-

tion of the walls of the pollen grain the cytoplasm of the tapetal cells becomes much vacuolated and the nuclei lose their chromatin; but at no time does the layer become broken. The parietal layers at the time of the tetrad division are three to five in number, the endothecium is thickened on its inner and lateral walls, and the epidermis is undifferentiated. The thickening of the endothecium walls takes places very late—simultaneously with the division of the pollen grain nucleus—the cells for some time previous to this being filled with starch.

Dehiscence is by means of two longitudinal slits, each of which opens two pollen sacs of the anther. A deep crease runs between each pair of pollen sacs upon the two sides of the anther, penetrating to the point at which the two microsporangia lie nearest each other (*fig. 13*). At this point is a group of small cells reaching from one microsporangium to the other, the walls of which are thrown into creases and folds, and fail to thicken in the further development of the anther, as do the neighboring cells.

The pollen mother cells apparently lie in the synapsis stage for several days. At their first division it is possible to count the chromosomes, the reduced number being twelve and their form short and blunt (*fig. 8*).

The tetrad division is simultaneous, there being no formation of wall after the first division. After a short period of adherence in tetrads the pollen grains round off and acquire the coats. The mature pollen grain is marked with eight meridional grooves so as to resemble a muskmelon. Beneath the grooves the intine is several times thicker than between the grooves (*fig. 11*). While the pollen grain is yet within the anther the nuclear division takes place which gives rise to tube and generative nuclei (*fig. 12*). In this condition the grains are shed, the stamens nearest the ovary opening first, and the outer ones successively.

OVULE AND MEGASPORE.

The placental outgrowths which arise from the flat sides of the ovary, at the point of juncture of the edges of the carpellary leaves, grow inward almost to the center of the ovary, and these I shall designate as the "main placental outgrowths" (*fig. 14*). Each

main placental outgrowth sends out two lateral outgrowths so as to resemble in cross section a letter T, in which the arms have been bent downward. Each pair of adjoining lateral outgrowths is closely appressed and directed backward toward the angles of the ovary. In the lower part of the ovary the adjacent lateral outgrowths fuse, but do not extend to the bottom, and in the upper part they do not reach the wall of the ovary as do the main placental outgrowths. Upon the edges of the lateral outgrowths and upon the surfaces lying next the main outgrowths are borne the ovules (*fig. 15*). The ovules at the base and top of the ovary lie parallel to the axis of the flower, those in the middle lie at right angles to it, the intermediate ones having intermediate positions according to their place in the ovary.

The summits of the carpellary leaves broaden and coalesce, and grow out in a direction radial to the axis of the flower, so that while their basal parts form the capsule and the stalk of the style, the tips form the umbrella of the style (*fig. 3*). The tip of each carpellary leaf organizes a very definite growing-point (*fig. 28*), and the portion between the tips nearly keeps pace in growth. Upon the ventral surface of each tip, just before it completes its growth, is formed the protuberance which bears the stigmatic surface.

The appearance of the primordia of the ovules upon the placentae takes place from the point opposite the angle of the ovary wall, where the adjacent lateral outgrowths meet, successively toward the angle formed by the lateral outgrowth and the main outgrowth (*fig. 19*). In vertical direction the development proceeds from the middle of the placenta toward top and bottom. The ovules first appear as protuberances initiated by the periclinal division of subepidermal cells and the accompanying anticlinal division of the epidermal cells, as is commonly the case. When the ovule first protrudes from the placenta there is no suggestion of a sporogenous cell. At this stage of development the winter rest intervenes. The first suggestion of a sporogenous cell comes with the enlargement of a single subepidermal cell, which is the megaspore mother cell (*fig. 16*). In three cases out of many hundreds examined there were two mother cells lying side by side. There is no tapetal cell. The bending by which the ovule becomes anatropous begins at once, and is quite

marked by the time of the appearance of the mother cell. Both transverse and longitudinal sections (*figs. 16* and *17*) show a double layer of cells at the sides of the mother cell, and median longitudinal sections show approximately five rows of cells in the ovule, exclusive of the epidermis.

The integument is single, its development beginning by periclinal divisions of subepidermal cells upon the convex side of the bending ovule, and continuing as a ring which grows rapidly on the side where it began first and slowly on the opposite side, which lies next the raphe. The rapid growth of the ovule is accomplished largely by the chalazal end. By the time of the first division of the mother cell the bending of the ovule is completed, the integument has grown so as nearly to close the micropyle, and the mother cell has increased in size and encroached upon the nucellar tissue so as to lie next the epidermal cells over the entire distal end (*fig. 20*).

The difference in the time of appearance of the ovules upon the different parts of the placenta causes a difference in the degree to which the integuments develop (*fig. 19*), and also a difference in the maturation of the mother cell, and the germination of the megaspore in ovules in the different parts of the placenta, a difference which long remains evident.

At the first division of the mother cell it was not found possible to count the number of chromosomes. The division is followed by the formation of a wall (*fig. 20*), and in about half the cases observed both the daughter cells again divide to form the normal linear tetrad of megaspores (*fig. 23*). In the remaining cases the micropylar daughter cell fails to divide, resulting in a series of three megaspores (*fig. 21*); and much less frequently the micropylar daughter cell divides by a wall parallel or nearly parallel to the long axis of the nucellus (*fig. 22*). In any case it is the chalazal megaspore which functions, the micropylar ones being appressed to the layer of nucellus and absorbed. The maturation of the megaspore is coincident with the tetrad division of the microspore mother cells.

EMBRYO SAC.

Such has been the elongation of the ovule by the time the megaspore matures that the nucellus is lengthened five or six times its diameter,

being made up of slightly elongated cells five or six rows thick in median section. The integument, about five cells thick, has now grown well beyond the tip of the nucellus, and its lips have become somewhat appressed to form the long micropyle. The cells in the innermost layer in the integument show active division in the direction of the greatest length of the nucellus, and by their dense protoplasm and large nuclei stand out prominently as a definite layer which I shall designate as the "columnar tissue."

After the disappearance of the megaspore sister cells the definitive megaspore continues its absorptive activity to the destruction of the single layer of nucellus at its micropylar end, so that the distal half of it comes to lie directly against the columnar tissue of the integument. The chalazal end is pointed, occupies at this time a median position in the nucellus, and is apparently active in the degeneration of the nucellar tissue, in accommodation to its own growth. About this time the definitive megaspore undergoes division. The daughter nuclei take places at opposite ends of the embryo sac (*fig. 24*), and quickly undergo the second (*fig. 25*) and third divisions in the normal manner.

The mature embryo sac is typical in every respect. It is elongated to four or five times its width, the sides lie next the columnar tissue and the base continues to be pointed and median. The synergidae lie side by side and the egg protrudes a little way below them, nearer the center of the sac. The cytoplasm of the synergidae is dense and stains heavily with the Flemming triple; that of the egg is greatly vacuolated. The antipodals lie well together in the conical base of the sac (*fig. 26*). The polar nuclei meet midway between the ends of the sac, and after their fusion the endosperm nucleus continues to occupy this position (*fig. 26*). After the fusion of the polar nuclei the endosperm becomes very active in the disorganization of the remaining basal portion of the nucellus. In this activity the antipodals do not take part. The base of the sac remains pointed, but from being median now comes to lie against the columnar tissue at one side of the nucellus by means of the absorption of the nucellar tissue which lay between its previous position and the columnar tissue. The further enlargement of the sac is accompanied by a pushing downward of the base between the nucellus and columnar

tissue, and in some preparations the antipodals would seem to have been pushed to one side (*fig. 27*). The columnar layer now shows its maximum development, being made up of deep, much-flattened cells with darkly staining cytoplasm. The function of these cells is no doubt that of secreting and passing over to the sac sugars or other elaborated foodstuffs.

POLLINATION AND POLLEN TUBES.

Pollination takes place, near Baltimore, during the first week in May. In the mature style of *Sarracenia* at the time of pollination the umbrella is a pale green color. Its internal structure is leaf-like without a definite palisade, but with abundant intercellular spaces and stomata numerous upon the upper surface and few upon the lower. Long unbranched unicellular hairs cover the lower surface so thickly as to form a tomentum in which considerable pollen is caught at the time of shedding. There are also upon both sides of the umbrella multicellular glands of spheroidal shape projecting slightly above the level of the epidermis. Running from the five stigmatic surfaces toward the center of the umbrella are heavy veins which comprise both vascular and conducting tissue.

The union of the carpels in the formation of the stalk of the style is such as to leave at its center a pentagonal cavity which in the mature flower connects the interior of the capsule with the external air. An examination of the veins of the umbrella two weeks before pollination will show the conducting tissue as a cylindrical strand about ten cells in diameter. The cells are much elongated, with pointed ends, or many cells of this description have divided transversely to two or four cells. The cytoplasm is dense, the nuclei are large, elongated, often three times as wide as long, binucleolate, and poor in chromatin. At the time of the passage of the pollen tubes the conducting strand has become enlarged to more than twice its previous diameter at the expense of the surrounding tissue, and the cells have become still more elongated. The cytoplasm is much vacuolated, the nuclei are attenuate at the ends and devoid of nucleoli (*figs. 32, 33*), and there are large intercellular spaces. The vascular tissue of the veins lies beneath the conducting tissue and is continuous with the vascular tissue of the styler stalk.

Two weeks before pollination transverse sections of the stalk of the style show five strands of heavy-walled cells running from the angles of the central cavity half way to the periphery (*fig. 34*). The tissue which these cells represent in cross section is four to six cells thick and runs the entire length of the stalk, being in the median line of the carpels. About the time of pollination these sheets of cells are found to split into two layers, which separate in such a manner as to form canals which are connected with the central cavity (*fig. 35*). The surface layer of cells on the interior of the canal becomes detached and undergoes partial degeneration. The five conducting canals thus formed are continuous with the conducting tissue of the veins of the umbrella above, and open below midway between the main placental outgrowths.

The stigmatic surface is richly provided with long, curved, heavy-walled outgrowths of epidermal cells (*fig. 31*), which serve to catch pollen and hold it. Pollen was found to be present in abundance on all stigmas examined. There is no definite sprouting-pore in the grains, but the tubes grow more commonly from the meridional grooves. The pollen tubes grow between the cells of the stigmatic surface and their entire passage is between the cells of the conducting tissue and never through them. They follow the well-defined course of the conducting tissue along the vein of the umbrella and down the stalk of the style (*fig. 30*).

The generative nucleus was not seen in any case to have divided before the sprouting of the pollen tube, and the earliest position in which it was seen to have divided was in a tube which had nearly reached the center of the umbrella. The tube nucleus is spherical and precedes the generative nuclei. The latter are alike in form—elongated and curved or often bent twice in serpentine manner. The distance of the nuclei from the end of the tube is four to six times the diameter of the tube. The cytoplasm is dense in the entire end and around the nuclei (*fig. 36*).

When the pollen tubes enter the cavity of the ovary from the five conducting tubes of the stalk, they are directly above the line of juncture of the two adjacent lateral placental outgrowths. The course of the pollen tubes is at first a downward one between these outgrowths, and later an outward one radial to the axis of the ovary

(fig. 30). In this manner the edges of the placentae are reached after a course in the ovary which, for the tubes growing to the lowermost ovules, is as much as 6 to 8^{mm}, and lies entirely outside the tissue of the plant in an ovary the cavity of which has direct communication with the external air. The epidermal cells of the placental surfaces between which the pollen tubes pass are densely filled with cytoplasm; beneath them lie three layers of flattened cells of similar contents. Thin transverse walls are formed in the tubes near the stigmatic surface (fig. 37), and far down in the ovary, near the ovules, plugs are not infrequent in the tubes, being three to six times the diameter of the tube in length.

The distance traversed by the pollen tubes which reach the lowermost ovules in flowers of average size, is about 4^{cm}. Provision for the nutrition of the tube during its growth and passage is perhaps made in part by the photosynthetic activity of the umbrella. Previous to pollination the epidermal, subepidermal, and some deeper cells of the umbrella are filled with densely-staining, finely granular contents. In fresh material of the same age the contents of these cells fail to react to tests for sugar made with Fehling's solution, *α*-naphthol and thymol, as well as to tests for starch. Similar contents fill the epidermal cells of the stalk of the style. The course of the tubes as far as their entrance to the ovary is doubtless through a strong solution of sugars. Below the point of entrance to the ovary the passage between the placental walls is probably through a film of sugary solution held there by capillarity and supplied with materials from the epidermal cells of the placental walls, which after pollination are highly vacuolated, in marked contrast to their condition before pollination.

FERTILIZATION.

The fusion of the male and female nuclei in fertilization is preceded by the division of the endosperm nucleus in nearly all the embryo sacs. Fertilization takes place, then, in all ovules at nearly the same time irrespective of a difference in the development of the endosperm due to the position of the ovule upon the placenta. As to the length of time intervening between pollination and fertilization I am unable to give any exact data. A visit on May 24 to plants

growing in the open found the anthers nearest the ovary to have shed their pollen. Material collected at the same locality two days later was found to show fertilization. The time of pollination of the particular flowers gathered and fixed may have been as much as five days before gathering, but was probably not earlier.

The thin-walled slender pollen tubes may be found in abundance about the mouths of the micropyles, often forming considerable masses. The cells which line the micropyle are heavy-walled and of such darkly-staining contents that it is difficult to observe the pollen tube within the micropyle, and indeed the entrance of the tip of the tube, with the nuclei, was not observed. The synergidae become appressed to the wall of the sac. The end of the tube upon entrance to the sac becomes expanded and pushes downward to one side of the egg. The generative nuclei have lost the elongated shape they were seen to have while passing down the style and have become spherical. Fusion of the first generative nucleus shows no special peculiarities (*fig. 38*).

ENDOSPERM.

The fusion of the polar nuclei is quickly followed by division. The first wall in the endosperm is transverse to the length of the sac and divides it into equal halves (*fig. 39*). The daughter nuclei divide in like manner (*fig. 40*), as do also the granddaughter nuclei, giving rise to an endosperm of eight cells in linear series, in which the walls are all transverse, although not uncommonly somewhat oblique (*fig. 41*). Subsequent divisions are less regular, and by the time the fertilized egg has divided the endosperm contains approximately 150 cells, its base having used up the nucellus either completely or all but a half dozen cells (*fig. 42*). At this time the endosperm cells are highly vacuolated and the laying down of food has not begun.

The relative rate of development of the endosperm in ovules upon different parts of the same placenta is the same as was noted with regard to the integuments. An ovule at the point of juncture of the adjacent lateral placental outgrowths may have an eight-celled endosperm at the same time that the endosperm nucleus has not yet divided in an ovule upon the edge of the placenta nearest the main placental outgrowth.

EMBRYO.

The first division of the fertilized egg is in a direction parallel with the length of the sac. The two-celled embryo (*fig. 43*), at first oval, becomes gradually elongated, divisions following in the same plane as the first, but not in a manner in which it has been possible to discover any regularity. After the embryo has attained a length of five to seven cells, there is a lateral division of the terminal cell (*fig. 44*), the beginning of the embryo proper. The suspensor is usually curved, though not always to so great an extent as shown in the figure. I have been unable by lack of material to observe stages in the development of the embryo immediately following the transverse division of the terminal cell.

In material of June 25 the embryo proper is found to have reached a size of approximately 250 cells, with ellipsoidal form (*fig. 45*). Dermatogen and perilem are well-defined, but no procambial cells have as yet appeared. The endosperm has by this time increased greatly in diameter, encroaching upon the tissue of the integuments. The endosperm cells have become well-stored with aleurone except in the central portion of the micropylar end—the region destined to be occupied by the full-sized embryo of the mature seed. In embryos as large as that shown in *fig. 45* the suspensor is surrounded by endosperm cells in which aleurone has been laid down; the embryo proper is surrounded by cells of highly vacuolated contents.

SEED AND SEEDLING.

Material gathered during the last week of July exhibits seeds which are practically mature. The embryo has grown to an elongated ellipsoidal form, the cotyledons being about one-third the length of the whole (*fig. 46*). Elongated procambium cells stretch from the basal end of the embryo to the region of the stem growing-point. Stomata are not formed in the embryo until the time of germination. A few endosperm cells at the sides and cotyledonary end of the embryo are free of aleurone, as they remain in the mature seed.

The surface layer of cells of the integument forms the seed coat. Its cells become irregular on their external surface and the walls are greatly thickened, with conspicuous pores in the lateral and basal walls, but none in the walls forming the surface of the seed

(fig. 47). The inner cells of the integument are all disorganized by the growth of the endosperm and reduced to a layer of the remaining walls of flattened cells. The raphe of the ovule develops into a wing upon one side of the seed, as seen in fig. 47. In the mature seed there is a coating of wax upon the surface which renders them unwettable, a condition in which they remain for several weeks after they have been placed in wet moss.

Provision for the shedding of the seed is made by a deep furrow surrounding the raphe just at its junction with the placenta (fig. 48). The dehiscence of the capsule is loculicidal and is provided for by a deep suture upon the external surface of the capsule wall at a point where the wall is traversed by a heavy vascular bundle. Dehiscence takes place late in September or early in October, the seeds are scattered gradually during many weeks by chance shaking of the scape by wind or animals. The old flower, with umbrella and sepals still persisting, is often found side by side with the bloom, of the following year.

On germination the seed is elevated above the soil or moss by growth of the hypocotyl, which is sharply bent and is the first part of the seedling to protrude. The tips of the cotyledons remain for some time in the seed, functioning as haustoria for the removal of the stored food of the endosperm. The tips of the cotyledons are active in the removal of the endosperm both at their ends and along their sides (fig. 49). The cotyledons expand to liguliform leaves about 1 cm long (fig. 50), and persist until about the time of the formation of the third epicotyledonary leaf. The cotyledons develop stomata during the process of germination and the epidermal and subepidermal layers of isodiametric cells bear chlorophyll.

DEVELOPMENT OF LEAVES.

The stem growing-point of *Sarracenia* is massive and acutely dome-shaped in the seedling (fig. 51). There is a definite layer of dermatogen and a common group of initials for periblem and plerome. The first epicotyledonary leaf arises opposite the interval between the cotyledons. It is finger-shaped with a somewhat broadened base. On reaching a length about twice its diameter there begins a rapid lateral outgrowth of the tissue of an 0-shaped area on the

side of the leaf rudiment which faces the growing-point, giving rise to a pit which is destined to become the cavity of the pitcher leaf (*fig. 52*). The basal part of the 0-shaped outgrowth now begins to grow upward, in which it is accompanied at the same rate by the upper portion of the 0, which at the same time carries forward the apical growth of the leaf (*fig. 53*). The cavity of the pitcher thus grows in depth by the upward growth of the tissue by which it is surrounded. The bottom of the cavity is subsequently elevated to some extent by the further growth of the tissue beneath it, but there is no sinking of the bottom of the cavity, considered as a possibility by ZIPPERER.² The entire early development of the leaf resembles closely that which has been described for *Darlingtonia californica* by GOEBEL.³

The first epicotyledonary leaf reaches its maximum size at a length of about 2.5^{cm}, and is slender in form, the cavity reaching well down toward its base, and the wing being but slightly developed. At the summit it is hooded in such a manner as to resemble the mature leaf of *S. variolaris*. The walls of the pitchers of the seedling are six to eight cells in thickness, with open mesophyll, chlorophyll in all the cells, and stomata over the entire external-epidermis. There are two principal strands of vascular tissue, one in the base of the wing and one on the opposite side of the pitcher, with smaller anastomosing strands between these. In the throat of the pitcher all the epidermal cells are produced into long projecting points; lower in the pitcher occasional epidermal cells, smaller than the others, give rise to long heavy-walled hairs, while in the bottom of the pitcher the epidermal and first layer of subepidermal cells are small and heavy-walled.

While each leaf of the young plant is passing through its period of most active growth, the internode between it and the next lower leaf is also elongating rapidly. A young leaf appears for this reason to arise from the petiole of the leaf below it (*fig. 51*). The relative elongation of the internodes is far greater in the seedling than in the adult plant.

The growth of a single plant from seedling to adult was not fol-

² Beitrag zur Kenntniss der Sarraceniaceen. Inaug. Diss. Erlangen. 1885.

³ Pflanzenbiologische Schilderungen II. 5:73-92. pls. 19-20. 1893.

lowed, but evidence points to the time requisite for the seedling to reach blooming age as being five or six years. Seeds of the crop of 1901, which in October of that year were placed in sphagnum in a loosely covered glass vessel, germinated in July 1902, and now, after 33 months, have no pitchers measuring over 2^{mm} in diameter. The extremely artificial conditions under which these seedlings were kept would make it inadvisable, however, to draw from them any general conclusions as to the rate of growth in the seedlings under natural conditions. The great number of intermediate stages in growth between the seedling and adult which may be observed in a single locality at any one season would also argue for the slowness of the plant in reaching adult size.

The stem growing-point of the adult plant is more broadly dome-shaped than that of the seedling, but is identical with it in the mode of origin of the dermatogen, periblem, and plerome. The earliest primordium of the leaf is likewise more massive than in the seedling, but essentially similar. Its form is conical, with a broadly semi-circular base embracing the growing-point. Near the summit, upon the side toward the growing point, is developed the narrow pit which is destined to form the cavity of the pitcher, its origin being due wholly to a difference in the rate of growth of the tissue at the bottom of the pit and that forming its sides (*fig. 54*). BAILLON⁴ in a brief note on the development of a *Sarracenia* (species not mentioned) has described this early stage and called attention to its similarity to an early stage in the development of peltate leaves, averring that "La membrane qui tapisse intérieurement l'urne n'est autre chose que l'épiderme supérieur de la feuille." This may be an entirely superficial analogy, or it may be a hint as to the ultimate origin of such a markedly modified leaf. GOEBEL (*l. c.*) has figured the early leaf primordium of *S. Drummondii*, which is essentially like that of *S. purpurea*.

With the continued growth of the leaf rudiment the pit becomes deeper, and its mouth becomes vertically elongated, although remaining very narrow. At stages somewhat earlier than that shown in *fig. 55*, the sides of the mouth of the pit have come together, closing it completely. *Fig. 55* represents a leaf primordium in which

⁴ (Note on the development of leaf of *Sarracenia*) *Adansonia* 9:380. 1870.

the wing is just beginning to appear. *Figs. 56-61* represent cross sections of the primordium at this age in the places indicated in *fig. 55*.

In older leaves, such as are represented in *fig. 62*, the base of the leaf primordium is stoutly crescentic in cross section. Through the groove at the inner side of the leaf base the next younger leaf appears (*figs. 55* and *62*). The groove becomes narrower and more shallow as we pass up the leaf and ends just short of the bottom of the cavity of the pitcher (*fig. 62*). Above the end of the groove there is a short portion of the young leaf which is circular in cross section, above which in turn the narrow flattened outgrowth of the wing has become more conspicuous. The wing rudiment ends rather abruptly at a point where retardation of growth in diameter indicates the line of demarcation between the pitcher and cover. The cavity of the pitcher at this stage reaches as far as the upper end of the circular portion of the base.

There have been many suggestions as to the homology of the parts of the pitcher leaf of *Sarracenia*. A view held by many is that the pitcher portion of the leaf is derived from the primordium of the petiole and the cover from the primordium of the lamina. GOEBEL (*l. c.*) points out that since there can be no distinction in the very young leaf of primordia of petiole and lamina there can be no line drawn as to what portions of the pitcher leaf "represent" these structures.

The anatomy of the mature leaf was first worked out by VOGL;⁵ it has more recently been reviewed by GOEBEL (*l. c.*), and minor contributions have been made by SCHIMPER⁶ (1882) and ZIPPERER (*l. c.*). The first leaf rudiments unfolded in the spring are aborted (*fig. 62*), consisting of the sheathing base surmounted by the minute retarded primordium of pitcher and cover. These are usually three in number, and may occur in plants which do not bloom, as well as in those which do. In the latter case the aborted leaves are those just above the one to which the flower appears to be axillary.

⁵ Die Blätter der *Sarracenia purpurea*. Sitzungsab. Wiener Akad. Wiss. Math.-Naturw. 50:281-301. pls. 2. 1864.

⁶ Notizen über insectfressende Pflanzen. Bot. Zeit. 40:225-234, 241-248. pl. 4 (*figs. 1-3*). 1882.

The axillary buds of *Sarracenia* are commonly very small and consist of growing-point and the primordium of a single leaf, completely covered and protected by the sheathing leaf base. An occasional axillary bud develops, the first two leaves being opposite and on the opposite sides of a line connecting the growing-point of the bud with the center of the shoot. There is thus brought about a branching of the rhizome, which by frequent repetition gives rise to large clusters of individuals.

The anatomy of the rhizome of *S. purpurea* has been described by ZIPPERER in sufficient detail, since it presents no unusual features. He has also given a correct account of the growing-point of the root and the development of the vascular tissue of the root: the growing-point being of the type in which the cap and three tissue layers are all derived from a common group of initials; the early order of vascular bundles being triarch.

Root hairs are few upon the roots of plants growing in a saturated substratum in the open, but are abundant in seedlings grown in highly saturated sphagnum, and in adult plants in the open which are growing in a substratum merely moist. Mycorrhiza has not been observed in *S. purpurea* in the vicinity of Baltimore, although fungal threads have been found covering the root of seedlings grown under the conditions previously mentioned and penetrating the epidermis. MACDOUGAL⁷ (1899) has described penetration of the epidermis by hyphae in adult plants without committing himself as to their mycorrhizal nature.

SUMMARY.

1. The flowers of *Sarracenia purpurea* are axillary, perfect, hypogynous, and radially symmetrical. The stamens are seventy to eighty in number and arise in ten groups. There are four microsporangia. There is a double layer of binucleate tapetal cells, derived from the primary archesporium. There are three to five parietal layers. The tetrad division is simultaneous; the microspore nucleus divides before the dehiscence of the anthers. The reduced number of chromosomes is twelve.

2. In the ovule there is a single archesporial cell, which is the megaspore mother cell. There is no tapetal cell. The ovule is

⁷ Symbiotic saprophytism. *Annals of Botany* 13:1-47. 1899.

anatropous and there is a single integument. The megaspore mother cell divides to a linear series of four megaspores, or after the first division the micropylar nucleus may fail to divide or may divide by a wall longitudinal to the ovule.

3. The chalazal megaspore is functional, and develops a typical eight-celled embryo sac. The polar nuclei fuse and the endosperm may become two to eight-celled before the complete fusion of male and female nuclei in fertilization.

4. The pollen tube grows through a definite conducting tissue in the upper expanded portion of the style, through schizogenic canals in the stalk of the style and between the placental outgrowths in the ovary. The generative nucleus divides before the tube has passed into the stalk of the ovary. Fertilization presents no peculiarities.

5. The embryo is elongated and straight, with cotyledons. The storage tissue is endosperm filled with aleurone. The seed coat is the external layer of the integument. The cotyledons function as haustoria in germination and survive as chlorophyll-bearing leaves.

6. The first epicotyledonary leaf is pitchered and arises from a finger-like primordium in which a cavity is developed by unequal growth.

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EXPLANATION OF PLATES III-V.

Abbreviations used: *ant*, antipodal; *arsp*, archesporium; *br*, bract; *cav*, cavity; *col t*, columnar tissue; *con c*, conducting canal; *con s*, conducting strand; *con t*, conducting tissue; *col*, cotyledons; *cov*, cover; *cp*, carpel; *der*, dermatogen; *d s*, dehiscing slit; *e*, egg; *em*, embryo; *en n*, endosperm nucleus; *e s*, embryo sac; *esp*, endosperm; *f n*, female nucleus; *g n*, generative nucleus; *int*, integument; *int i*, integument initials; *l*, leaf; *l p o*, lateral placental outgrowth; *meg mc*, megaspore mother cell; *meg sc*, megaspore sister cell; *mic mc*, microspore mother cell; *micsp*, microsporangium; *mn*, male nucleus; *m p o*, main placental outgrowth; *nuc*, nucellus; *ov*, ovary; *par c*, parietal cells; *pet*, petals; *pn*, polar nuclei; *ppi*, initials of periblem and plerome; *pro c*, procambium cells; *sc*, seed coat; *sep*, sepal; *st*, stamen; *stg s*, stigmatic surface; *stk*, stalk of style; *sus*, suspensor; *syn*, synergid; *tap c*, tapetal cells; *tn*, tube nucleus; *um*, umbrella of the style; *w*, wing.

All figures are camera drawings from microtome sections except *figs.* 29, 30, 50, 55, and 62, which are from free-hand drawings.

PLATE III.

FIG. 1. Vertical section of young flower bud. $\times 30$.

FIG. 2. Transverse section of young flower bud of same age as in *fig. 1*; dotted outline represents position of carpel tips in higher sections. $\times 30$.

FIG. 3. Vertical section of older flower bud. $\times 30$.

FIG. 4. Transverse section of young stamen. $\times 232$.

FIG. 5. Transverse section of single microsporangium of older stamen. $\times 232$.

FIG. 6. Transverse section of portion of microsporangium and wall in microspore mother cell stage. $\times 400$.

FIG. 7. Transverse section of portion of microsporangium and wall with microspore mother cells in synapsis. $\times 232$.

FIG. 8. Transverse section of microsporangium and portion of wall; pollen mother cells in mitosis. $\times 400$.

FIG. 9. Pollen mother cells in metaphase of first mitosis. $\times 400$.

FIG. 10. Tetrads of microspores. $\times 400$.

FIG. 11. Pollen grain. $\times 400$.

FIG. 12. Pollen grain after division of nucleus. $\times 400$.

FIG. 13. Transverse section of mature anther. $\times 20$.

FIG. 14. Transverse section of young ovary. $\times 20$.

FIG. 15. Transverse section through middle of nearly mature ovary. $\times 7$.

FIG. 16. Longitudinal section of ovule with megaspore mother cell. $\times 400$.

FIG. 17. Transverse section of ovule through megaspore mother cell. $\times 400$.

FIG. 18. Longitudinal section of ovule with megaspore mother cell and integument. $\times 232$.

FIG. 19. Transverse section of single lateral placental outgrowth, showing difference in rate of development of integument on different parts of the placenta; somewhat diagrammatic. $\times 40$.

PLATE IV.

FIG. 20. First maturation division of megaspore mother cell. $\times 400$.

FIG. 21. Linear series of three megaspores, arising by failure of micropylar daughter cell to divide. $\times 400$.

FIG. 22. Tetrad of megaspores in which the micropylar daughter cell has divided longitudinally. $\times 400$.

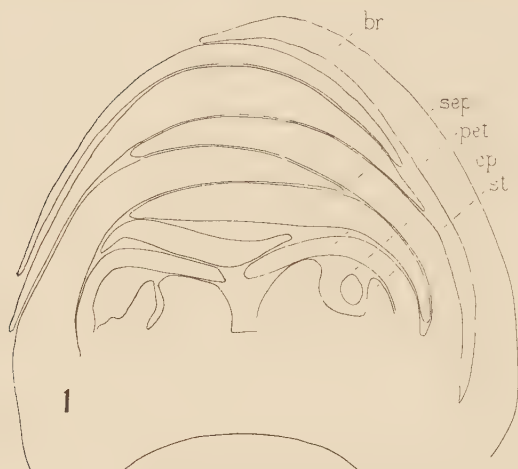
FIG. 23. Longitudinal section of ovule, with tetrad of megaspores, chalazal one enlarging and encroaching on single layer of nucellus. $\times 120$.

FIG. 24. Longitudinal section of portion of ovule showing two-celled embryo sac, nucellus, and columnar tissue. $\times 232$.

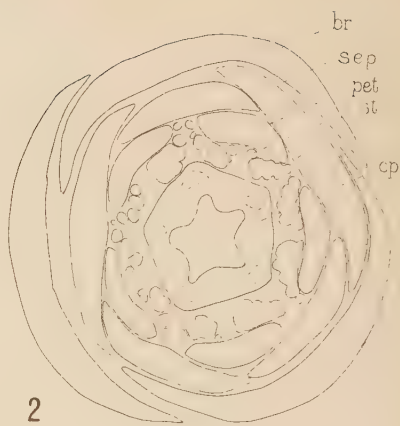
FIG. 25. Longitudinal section of portion of ovule showing four-celled embryo sac. $\times 232$.

FIG. 26. Longitudinal section of portion of ovule showing fully developed embryo sac. $\times 400$.

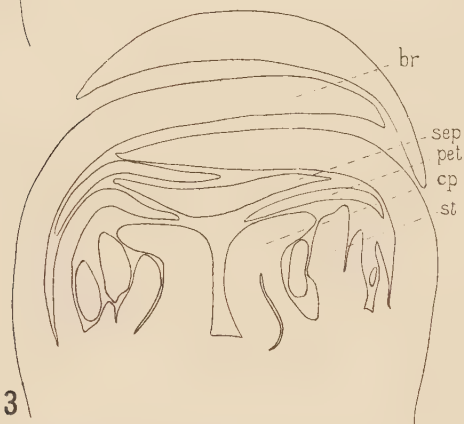
FIG. 27. Longitudinal section of portion of ovule showing embryo sac after fusion of polar nuclei; antipodals pushed to one side. $\times 232$.



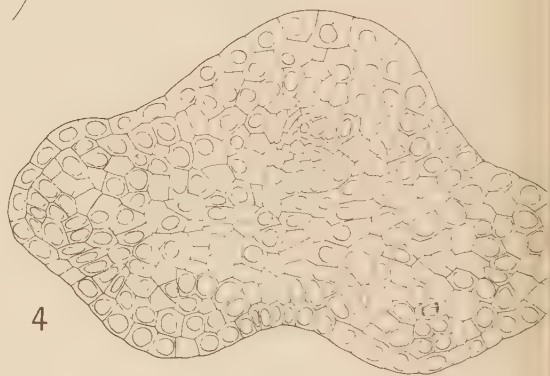
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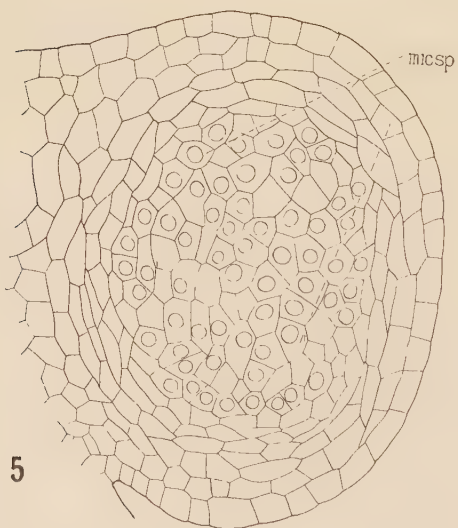
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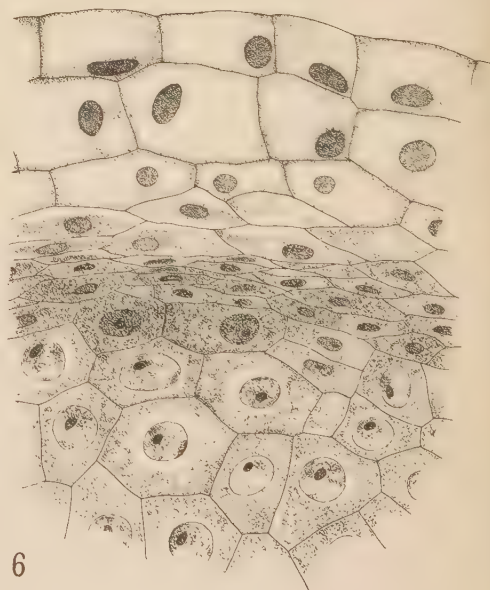
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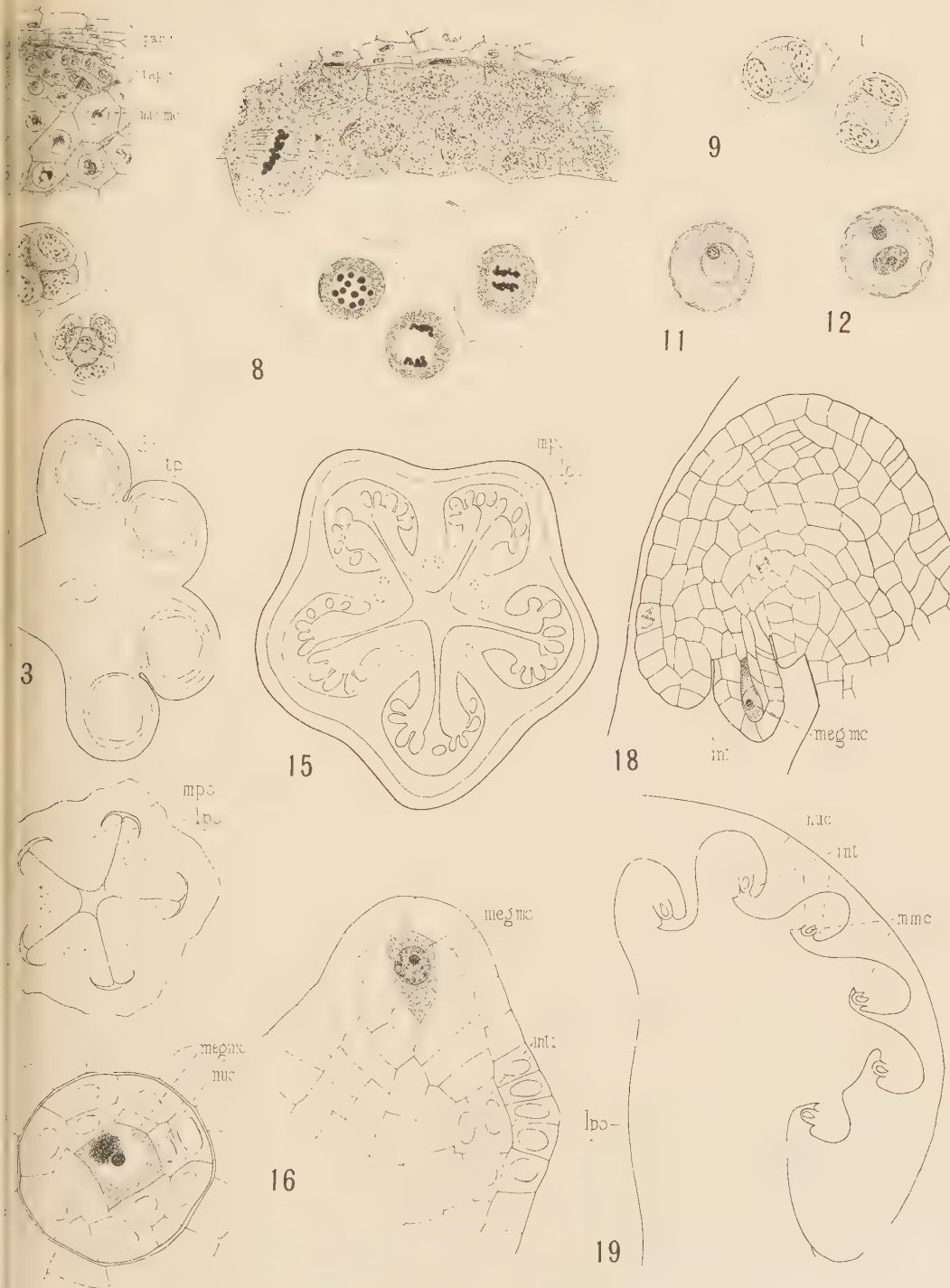


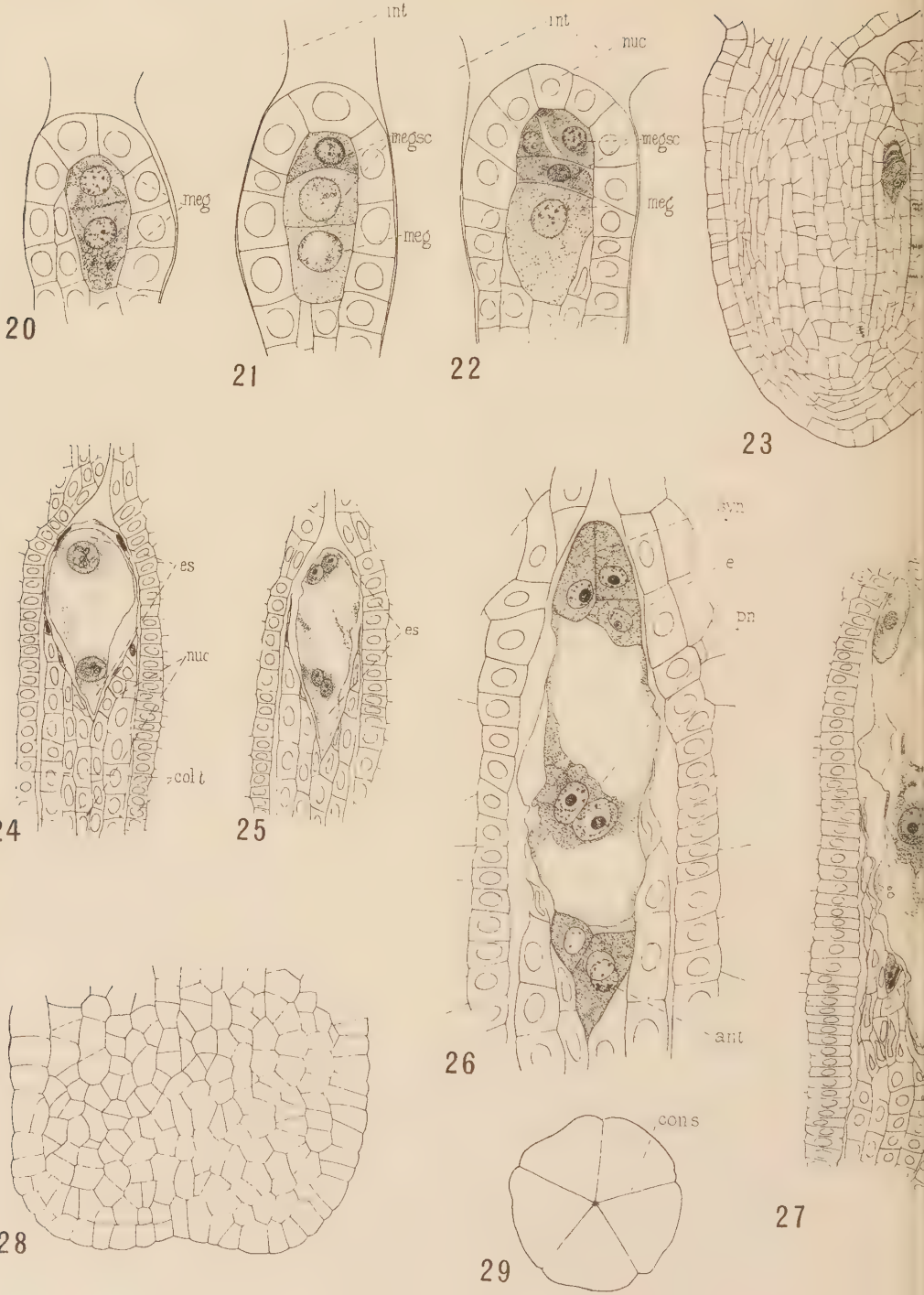
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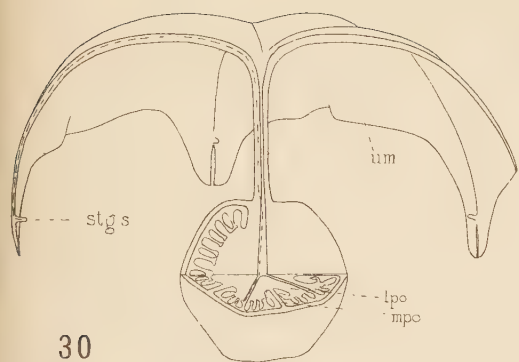


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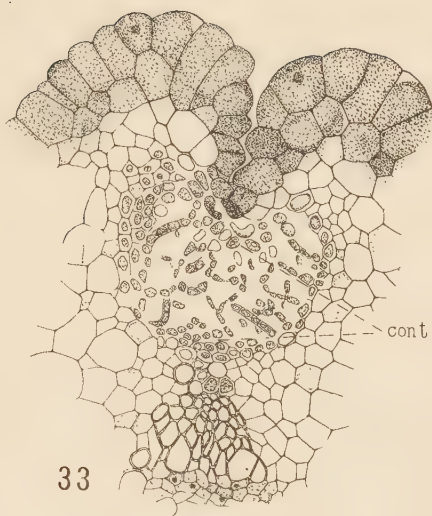
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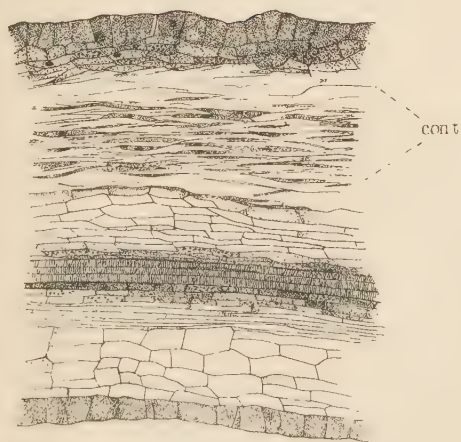
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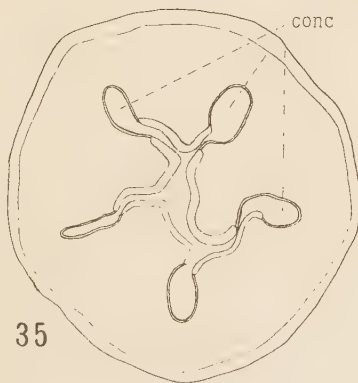
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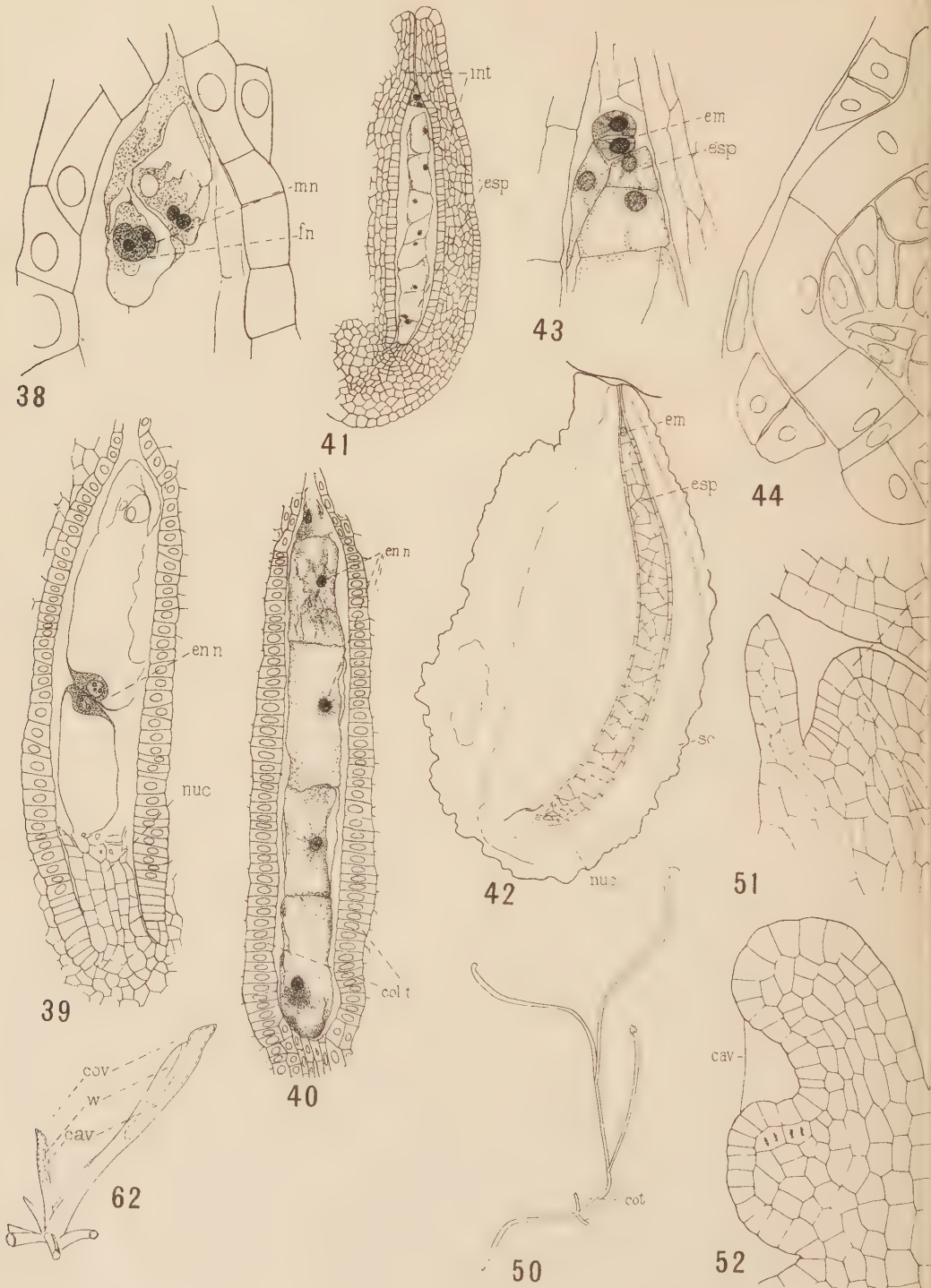
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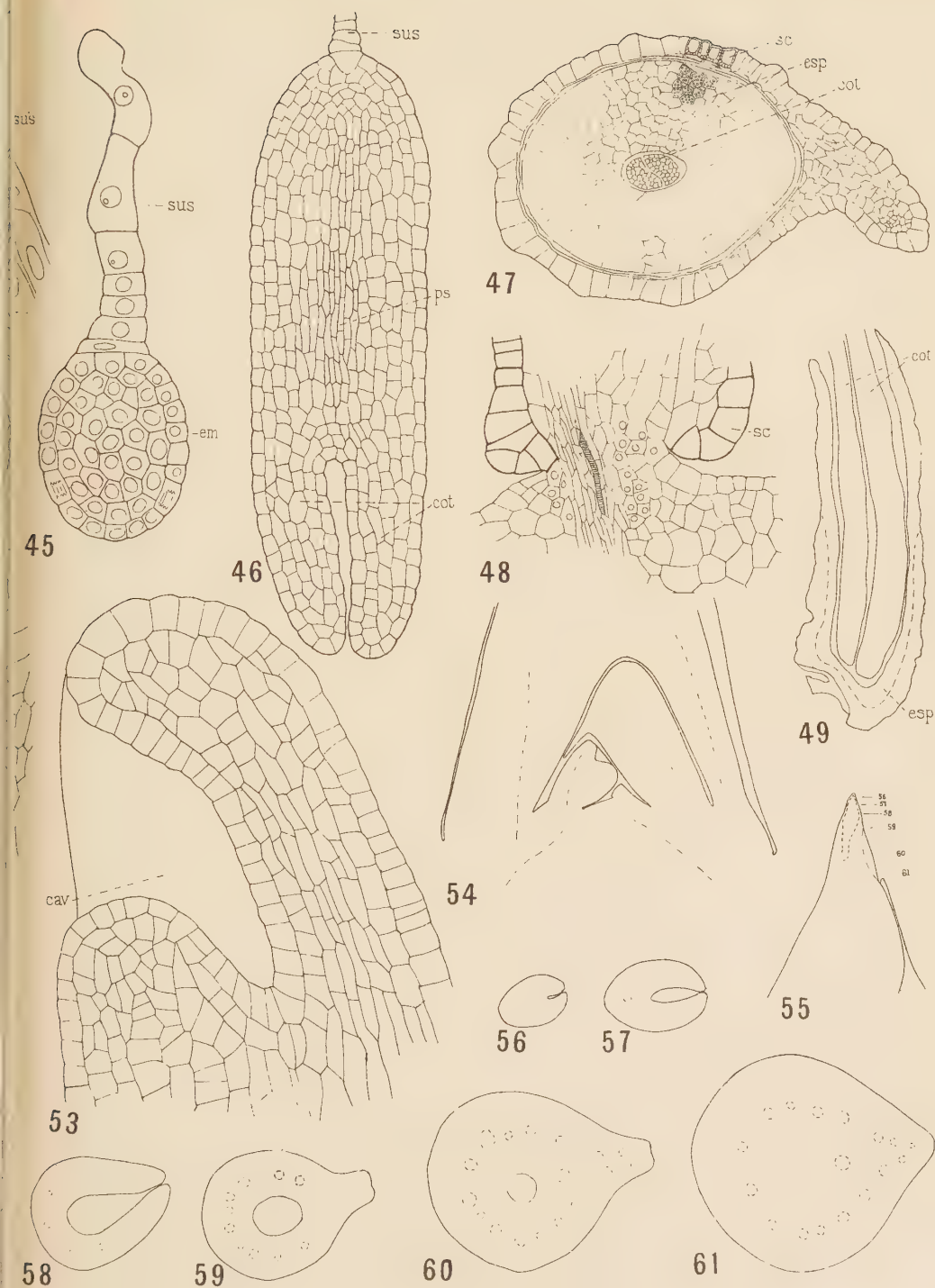


FIG. 28. Growing point of tip of carpel in umbrella, horizontal section. $\times 40$.

FIG. 29. Stylar umbrella viewed from above; in outline. $\times \frac{2}{3}$.

FIG. 30. Ovary and style to show the course of pollen tube indicated by dotted line; somewhat diagrammatic. $\times 2$.

FIG. 31. Longitudinal section of stigmatic surface with sprouting pollen grains. $\times 120$.

FIG. 32. Longitudinal section of conducting strand in umbrella of style showing conducting and vascular tissue. $\times 40$.

FIG. 33. Transverse section of upper surface of umbrella of style showing conducting and vascular tissue and glandular epidermis. $\times 120$.

FIG. 34. Transverse section of stalk of style before pollination. $\times 20$.

FIG. 35. Transverse section of stalk of style at time of pollination. $\times 20$.

FIG. 36. Tip of pollen tube from conducting tissue of umbrella; optical section. $\times 400$.

FIG. 37. Cross wall in tube near stigmatic surface. $\times 400$.

PLATE V.

FIG. 38. Longitudinal section of upper end of embryo sac showing fusion of male and female nuclei. $\times 400$.

FIG. 39. Longitudinal section of embryo sac showing two-celled endosperm, columnar tissue, and remains of nucellus. $\times 120$.

FIG. 40. Longitudinal section of embryo sac showing four-celled endosperm. $\times 120$.

FIG. 41. Longitudinal section of portion of ovule showing eight-celled endosperm and integument. $\times 40$.

FIG. 42. Longitudinal section of seed through the wing showing multicellular endosperm and two-celled embryo. $\times 20$.

FIG. 43. Two-celled embryo. $\times 232$.

FIG. 44. Young embryo with suspensor. $\times 400$.

FIG. 45. Older embryo with suspensor. $\times 232$.

FIG. 46. Longitudinal section of embryo from mature seed. $\times 120$.

FIG. 47. Transverse section of mature seed cutting the embryo through the cotyledons; detail partially filled in. $\times 40$.

FIG. 48. Longitudinal section through the hilum of nearly mature seed. $\times 120$.

FIG. 49. Longitudinal section of germinating seed, with cotyledons; seed coat has been removed; portion beyond the dotted line is that from which aleurone has not yet been removed. $\times 20$.

FIG. 50. Seedling with cotyledons and three epicotyledonary leaves. $\times 1.5$.

FIG. 51. Vertical section through growing-point of seedling. $\times 232$.

FIG. 52. Median vertical section through primordium of first epicotyledonary leaf. $\times 232$.

FIG. 53. Median vertical section through portion of primordium of first epicotyledonary leaf in later stage of development. $\times 232$.

FIG. 54. Vertical section through growing point and young leaves in adult plant. $\times 20$.

FIG. 55. Surface view of primordium of leaf seen from the side, next younger leaf also showing; dotted outline marks cavity of leaf. $\times 3$.

FIG. 56. Transverse section of leaf in *fig. 55* at *56*. $\times 20$.

FIG. 57. Transverse section of leaf in *fig. 55* at *57*. $\times 20$.

FIG. 58. Transverse section of leaf in *fig. 55* at *58*. $\times 20$.

FIG. 59. Transverse section of leaf in *fig. 55* at *59*. $\times 20$.

FIG. 60. Transverse section of leaf in *fig. 55* at *60*. $\times 20$.

FIG. 61. Transverse section of leaf in *fig. 55* at *61*. $\times 20$.

FIG. 62. Later stages of young leaves; cavities shown by dotted outline. $\times 1$

VITA.

FORREST SHREVE was born at Easton, Maryland, in 1878; received his early education at the Friend's Select School, Easton; the Easton High School, and the George School, Newton, Pennsylvania. He received the degree of Bachelor of Arts at the Johns Hopkins University in 1901, entering the graduate department in the same year. His subjects have been Botany, Zoölogy, and Physical Chemistry. He was holder of a University Fellowship in 1904-5.

